SPITE, ALTRUISM, AND SEMANTICS: A REPLY TO WALTZ

I basically agree with Waltz's (1981) contention that problems exist in discussions of spite and altruism which result from imprecise definitions of these terms. However, it is also my feeling that some of these problems are exacerbated by unrealistically narrow interpretations of observed phenomena.

For example, in Waltz's precise definition of reciprocal altruism, three elements are assumed to be inherent: (1) one individual aids another (2) in anticipation that the recipient will return the favor, i.e., reciprocate; and (3) that the original actor benefits at some time in the future, either directly or indirectly. As Waltz points out, there also exists a broad definition of reciprocal altruism that comprises only elements 1 and 3. However, the crucial aspect of the precise definition is that altruistic individuals must be able to distinguish between conspecifics who will reciprocate and those who will not, i.e., cheaters.

There are at least two major problems associated with this last assumption. First is the means by which an individual reciprocates. As Waltz points out, "There is no need for the actor (altruist) to be repaid directly by the recipient of its act, nor is it necessary for the debt to be repaid in kind." Recognition of this should also lead to the realization that reciprocity may be difficult to identify. Second, the recognition of cheaters implies that the phenomenon in question has either (1) been in existence long enough for selection to have acted upon it, (2) been a regular enough occurrence for there to have been selection against cheaters, or (3) been costly enough to require selection to recognize cheaters. If all of these criteria are not met, there may simply not be any strong selective pressure to recognize cheaters and if the costs to individuals of altruistic acts are minimal, a low level of cheating might well be tolerated in a social species (Wilson 1980, chap. 3).

However, despite these arguments, I believe that the data described in my original (1980) paper meet the criteria set forth by Waltz in his precise definition of reciprocal altruism. There can be little doubt that a "stepmothering" female gull is performing an act which involves risk. She is expending considerable time and energy in caring for the offspring of another female, with a finite chance that she will not be able to mate with the father of those offspring in subsequent years. Either she or her new mate could die before the next breeding season (average annual mortality in adult gulls is about 10%–20%; Kadlec and Drury 1968; Hunt et al. 1980; author's unpublished observation), or the male could refuse to mate with her in subsequent seasons. Male western gulls have been observed to pair with a female for a short period, ranging from less than an hour to several weeks, and then either to abandon the female or drive her away (Pierotti 1981; J. C. Wingfield, personal communication). In any case, there is at least a 20%–30% chance (10% for the female and 10%–20% for her mate) that she will not be able to mate with the male during the next breeding season, simply because one of them may not survive until the next breeding season.

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With regard to the detection of cheaters, it is clear that Waltz has not considered the situation carefully. The only potential cheaters are the male gulls, who could drive the stepmother away after using her. The male reciprocates by allowing the stepmother to remain on the territory, and possibly by allowing her to be his mate in future years. If she fails to help him raise young, he would be less likely to remain paired to her. It has been demonstrated in gulls that the major cause of separation of pairs is failure to raise offspring; whereas pairs that successfully raise offspring almost never separate (Coulson 1972; Pierotti 1976, 1979). The male is also taking a risk by allowing a strange female to remain alone on the territory with his eggs or chicks. The female could either ignore the eggs or chicks, or in an extreme case, could even kill or eat them, or drive the chicks away, since she has no investment in them to begin with.

As for Waltz's contention that female cheaters would be impossible to detect, it is my feeling that this situation would never arise. There are only two ways that a female could cheat in this manner. One way would be to die, which is clearly nonselective. The other is to desert her mate after laying eggs and to enter the pool of unpaired females, a solution which leaves her no better off than the stepmother she is exploiting.

The problems which I referred to earlier in this paper concerning the nature of reciprocity and the detection of cheaters are apparent in Waltz's discussion of my examples. With regard to stepmothering, there are several potential benefactees of the stepmother's aid. First, the deceased or departed female benefits, but she cannot reciprocate. Second, the mate benefits, and he may reciprocate in several ways, either by allowing the female to share his territory during that breeding season, by providing her with food and protection, or by pairing with her in subsequent years. Of these alternatives, only the last involves any selfishness on the part of the male. Finally, the chicks benefit from the care of the stepmother and they may reciprocate, either by providing an inexperienced female with experience which she could put to good use in raising her own offspring, or possibly by functioning as part of a family social group away from the breeding colony at some later date (author's unpublished observation).

Likewise, concerning chick adoption and creching, there are at least two potential sets of benefactees from this behavior: (1) the parents whose chicks are cared for and (2) the chicks themselves. Most adult gulls appear to readily adopt and care for chicks other than their own (Holley 1981; Graves and Whiten, in press and references therein). Since the benefits of having chicks which are inadvertently lost cared for by other adults are obvious at both the individual and population levels (Holley 1981), the cost of the few individuals which cheated on the system and refused to adopt could simply be sustained at a low level. There would be little or no benefit, however, to those individuals which attempted to cheat by passing their offspring on to neighbors, since there is a very real risk that young chicks might be eaten once they leave the natal territory (Parsons 1971). In addition, parent gulls are often unable to raise even two or three offspring in any given year. Gulls that attempted to cheat by driving off their first brood, as suggested by Waltz, would be risking total loss of this brood. In addition, the breeding season in gulls is timed so that chicks hatch when food availability is

high. Therefore, to delay raising a brood for a month while incubating a second clutch after driving away a first brood would almost certainly reduce the fitness of birds that opted for this strategy. It is well known that gulls breeding later in the season show greatly reduced hatching and fledging success (Parsons 1975; Hunt and Hunt 1976; Pierotti 1979 and references therein). Similarly, cheaters at creches would be reducing the amount of food received by all chicks. As a result, they would be reducing the chances of survival of their own offspring.

Waltz's statements concerning rates of immigration, emigration, and philopatric dispersal in seabird breeding colonies refer to terns (Nisbet 1978) and albatross (Fisher 1976). A large body of literature exists for gulls which suggests that the vast majority of young gulls do not return to their natal colony to breed (Olsson 1958; Drost et al. 1961; Spaans 1971; Coulter 1975; Chabrzyk and Coulson 1977). This apparently occurs because young birds are often unable to establish themselves in crowded natal colonies such as Southeast Farallon or the part of Great Island where creching was observed. Under such circumstances in a long-lived species, site tenacity, and colony fidelity on the part of established adults may actually act to reduce the interrelatedness of individuals within a breeding colony. Thus, although it is possible that kin selection might play a factor in adoptions and creching, I consider it unlikely, especially given the spiteful behavior of many gulls directed at their neighbors.

Waltz is certainly correct in pointing out that spiteful behavior does not gibe with philopatric dispersal, especially where piracy and the killing of neighboring chicks are concerned. It is difficult to imagine how a bird which has lost its own offspring can improve its fitness by killing the offspring of its relatives.

Concerning the issue of intraspecific piracy. Waltz contends that the data do not distinguish between cause and effect. However, an examination of table 4 (Pierotti 1980) will show that some pirates were capable of raising three or even four chicks without pirating, but switched to piracy in years when they had lost their chicks early in the season. In particular, male #10 (Pierotti 1980, table 4) fledged four chicks (2 of his own plus 2 adoptees), and had the highest feeding rate of any male observed during the study. In 1973, however, male #10 became a pirate after losing two of his three chicks shortly after hatching. In addition, since male #10 adopted both chicks from pairs that he had robbed in 1973 as a pirate, this undermines Waltz's suggestion that an individual could distinguish between relatives toward whom it would behave altruistically, and nonrelatives. All pirate males appeared to be perfectly capable of obtaining food by more conventional means and took no longer in foraging trips than males that obtained all their food by foraging at sea (Pierotti 1976, 1981).

With regard to spite, I again have a problem with Waltz's narrow definition, in which he contends that a behavior must either be selfish (actor gains, recipient loses) or spiteful in a narrow sense (both lose), and that situations where the actor is not harmed, but the recipient loses do not exist. This presents at least two difficulties. First, it seems eminently possible that situations could arise where the cost to the actor is effectively cancelled by the benefit to the actor, although perhaps not in a precise caloric sense. Second, where both spite and altruism are concerned, risk is an important, but essentially unmeasurable, aspect (in precise

quantitative terms). If an individual performs an act that involves a high risk of death or serious injury and escapes unscathed, how is its investment to be measured? I would argue that an individual which took such a risk to harm a conspecific would be spiteful, even if the cost of the specific act turned out to be low relative to benefits, either immediate or potential.

Waltz's narrow definition of spite is, therefore, not adequate for dealing with the killing of chicks. It is not necessary to demonstrate a loss of fitness to an individual which behaves spitefully, but even so, such risks exist. A male gull which enters another gull's territory risks a fight with the resident birds, which are at their most aggressive when defending their offspring. In addition, a fledged or nearly fledged gull chick can be a formidable opponent for an adult gull. Gull chicks grow to be as large and heavy as their parents before fledging, and will often defend the natal territory against intruding adults when their parents are absent (personal observation). The data of Davis and Dunn (1976) support the existence of spite. Also, Hand (1980) observed yellow-legged western gulls (*Larus occidentalis livens*) which had lost their eggs or chicks to attack other breeding conspecifics. During these attacks, while one bird engaged the resident adult in combat, others attacked (and often killed) the chicks of that adult. Since the risk involved to the spiteful birds is obvious in this instance, I feel that selfish behavior can be rejected as an alternative.

To conclude, I believe that Waltz has either misread or misinterpreted my arguments, and that his definitions of both spite and reciprocal altruism are unrealistically narrow. Wilson (1980, pp. 29–45) has argued convincingly that "weak altruism" (altruistic acts which are not costly to the performer, but which definitely benefit the recipient more than the performer) may be relatively common. I would consider most of the altruistic acts which I have described as being examples of "weak altruism," and possibly subject only to "neutral" selection (Wilson 1980).

I agree with Waltz that ethologists should fully consider alternative interpretations of behavior. However, Waltz fails to appreciate that I was attempting to operate within the context of inclusive fitness, and that in general, most of my explanations deal with the possible selective value of apparent nonselective behavior. It is also well for us to realize that there are pitfalls involved in optimization arguments (Lewontin 1978; Maynard Smith 1978). Therefore, rather than invoking kin selection or selfish individual behavior as Waltz appears to, it might be worthwhile to consider that animals may behave in a fashion which may have either no effect or a negative effect on their individual fitnesses. As Wilson (1980, p. 43) has pointed out, "There is already a trend toward renaming all forms of altruism that can evolve as 'genetic selfishness,' which presumably reserves the term 'altruism' for anything that can't evolve."

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